PREDATION ON DIURNAL INSECTS BY THE EASTERN HORSESHOE BAT, *RHINOLOPHUS MEGAPHYLLUS* GRAY (CHIROPTERA: RHINOLOPHIDAE)

CHRISTOPH R. PAVEY AND CHRISTOPHER J. BURWELL

Pavey, C.R. & Burwell, C.J. 1998 06 29: Predation on diurnal insects by the Eastern Horseshoe Bat, *Rhinolophus megaphyllus* (Chiroptera: Rhinolophidae). *Memoirs of the Queensland Museum* 42(2): 555-558. Brisbane. ISSN 0079-8835.

Insectivorous bats exhibit crepuscular activity despite being very vulnerable to predation by diurnal birds at such times. For this behaviour to persist the benefit(s) of crepuscular activity must balance or outweigh the costs. This study established that the Eastern Horseshoe Bat, *Rhinolophus megaphyllus*, captured diurnal insects from three orders; butterflies (Lepidoptera), dragonflies (Odonata) and cicadas (Hemiptera), during crepuscular activity. Diurnal prey were eaten at four roosts in eastern Queensland where prey remains were regularly collected and at three roosts where remains were collected opportunistically. The amount of predation on diurnal insects varied between the four roosts, and overall it was low. The emergence time of *R. megaphyllus* also varied between roosts with bats emerging earlier in rainforest than woodland. Earlier emergence occurred at the roost where predation on diurnal insects was most frequent. This study indicates that a possible benefit of crepuscular activity to *R. megaphyllus* is the availability of diurnal insects as prey. □ *Rhinolophus megaphyllus, predation, diurnal insects, crepuscular activity.*

Chris R. Pavey, 64 Arafura Street, Upper Mt Gravatt, Queensland 4122, Australia; Chris J. Burwell, Queensland Museum, PO Box 3300, South Brisbane 4101, Australia; 1 November 1997.

Many species of insectivorous bats have crepuscular activity, whereby they depart from their roosts during the period of civil twilight after sunset but prior to dark (Jones & Rydell, 1994). Insectivorous bats appear to be very vulnerable to predation by diurnal and crepuscular birds at such times (Young, 1980; Neuweiler et al., 1987; Speakman, 1991, 1995; Fenton et al., 1994; Jones et al., 1995). Bats are available as prey to diurnal and crepuscular birds only during the short time period at dusk and dawn when the activity rhythms of predator and prey overlap. Because diurnal and crepuscular birds can hunt only in daylight, twilight or moonlight, insectivorous bats could avoid predation by emerging after dark (Erkert, 1978; Black et al., 1979; Fenton, 1995). However, the evolution of a predator such as the Bat Hawk, *Macheiramphus alcinus* Bonaparte, with specialised adaptations for the capture of bats at dusk (Fenton et al., 1977; Black et al., 1979; Fenton, 1995), clearly demonstrates that crepuscular activity has persisted over evolutionary time.

The costs associated with crepuscular activity must be balanced or outweighed by benefits for the behaviour to persist. One potential benefit is that bats have access to diurnal insects, a term here used to include both diurnal and crepuscular species, during the dusk period (Black et al., 1979; Fenton et al., 1994). If this interpretation is correct, bats that show crepuscular activity should regularly capture diurnal insects. The current study sought to examine this possibility by determining the amount of predation on diurnal insects by the Eastern Horseshoe Bat, *Rhinolophus megaphyllus* Gray, 1834, a species of insectivorous bat known to be active at dusk.

METHODS

STUDY SPECIES. *Rhinolophus megaphyllus* is a relatively small bat (7-14g) which occurs in eastern Australia from Cape York Peninsula to central Victoria. This species captures insects using CF-FM (constant frequency-frequency modulated) echolocation calls emitted at high duty cycles (Jones & Corben, 1993; de Oliveira & Schulz, 1997). A large amount of experimental and observational evidence indicates that the echolocation calls of members of the genus *Rhinolophus* restrict them to the capture of insects that are either flying or sitting with fluttering wings (Link et al., 1986; Neuweiler et al., 1987; Rübsamen et al., 1988; Neuweiler, 1989, 1990; Emde & Schnitzler, 1990). This restriction is also likely to apply to *R. megaphyllus* (Pavey, 1995), so it cannot capture diurnal insects resting on foliage at night. Therefore, any diurnal insects in the diet are almost certainly captured when the insects are active.

FIELD SITES. The study was conducted at roosts of *R. megaphyllus* located in disused mines in eastern Queensland. Dietary data were collected from four roosts which, from S to N, were at Anduramba (27°09'S, 152°07'E), Conondale Ra. (26°39'S, 152°39'E), Irvinebank (17°26'S, 145°12'E) and Atherton (17°20'S, 145°26'E). Collections were made on 17, 19, 3 and 8 visits, respectively, to each roost. In addition, diurnal insects were found among prey remains in roosts at Mt Molloy (16°43'S, 145°20'E), Herberton (17°24'S, 145°24'E), Paluma (19°01'S, 146°13'E) and Iron Ra. (12°43'S, 143°18'E). Collections were made during a single visit to each of these roosts. The Conondale Ra., Paluma and Iron Ra. roosts were located within rainforest, whereas other roosts were located in eucalypt open forest or woodland. All sites were located away from sources of artificial light that may have attracted diurnal insects. None of the species of diurnal insects recorded as prey of *R. megaphyllus* in this study were observed in any of the roosts.

DIETARY DATA. The incidence of diurnal insects in the diet was determined by identifying remains of prey discarded by bats which had returned to diurnal roosts to feed. Prey remains, mostly wings, were collected by thoroughly searching the floor of each roost using a head torch. Remains were identified by comparison with pinned specimens at the University of Queensland Insect Collection and Queensland Museum. Most wings could be identified to family, and most lepidopteran material to species or genus. The minimum number of individuals of each prey taxon in each collection (site and date specific) was calculated by using the forewing or hindwing with the highest count.

Entomological literature was the source for verifying the activity rhythms of prey taxa that were potentially diurnal. The following texts were the primary references employed; Common, 1990 (Lepidoptera, excluding superfamily Papilionoidea); Common & Waterhouse, 1981 (superfamily Papilionoidea – butterflies); Watson et al., 1991 (Odonata); Moulds, 1990 (Cicadidae); CSIRO Division of Entomology, 1991 (other orders). If no information was available on the activity rhythms of a particular species or genus, it was assigned the activity pattern that was most characteristic of its family.

EMERGENCE TIME OF BATS. The time of departure was recorded for the colonies of *R. megaphyllus* at Anduramba (7 nights) and Conondale Ra. (3 nights), but not at Irvinebank or Atherton. Observations were conducted on nights with no rain or strong wind and during all phases of the moon. An observer, positioned within 20m of the entrance of each roost, counted the bats as they emerged in the evening. The time of first emergence was recorded, and also the time of darkness (when he was no longer able to see well enough to walk without the aid of artificial light).

TABLE 1. List of diurnal families and species of insects captured by *Rhinolophus megaphyllus* (n=35 prey items). A damselfly (Order Odonata, Suborder Zygoptera) from Conondale Ra. that could not be identified to family is not included.

Order/Family	Species	Sites (No. Taken)
Lepidoptera		
Hesperiidae	*Hasora khoda*	Conondale Ra. (1)
	Euschemon rafflesia	Paluma (1)
	Chaetocneme beata	Conondale Ra. (9)
Pieridae	*Eurema* sp.	Mt Molloy (1)
Nymphalidae	*Melanitis leda*	Conondale Ra. (1) Mt Molloy (1)
	Hypocysta adiante	Atherton (1)
Lycaenidae	*Hypochrysops miskini*	Atherton (1)
Odonata		
Aeshnidae	*Antipodophlebia asthenes*	Conondale Ra. (2)
	Austrogynacantha or *Gynacantha* sp.	Iron Range (1)
	unidentified spp.	Conondale Ra. (4) Mt Molloy (1) Iron Ra. (1)
Libellulidae	*Agrionoptera* sp.	Iron Ra. (1)
	Tholymis tillarga	Iron Ra. (1)
	Orthetrum sp.	Anduramba (1)
Hemiptera		
Cicadidae	unidentified spp.	Conondale Ra. (2) Atherton (2) Irvinebank (2)

RESULTS

DIET. A total of 830 insects was recorded among prey remains of *R. megaphyllus* at the four roosts. The number of prey items and number of diurnal insects recorded at each site were: Anduramba, 118 prey items (1 diurnal insect); Conondale Ra., 471 (20); Irvinebank, 53 (2); and Atherton, 188 (4). Diurnal insects made up 3.25% (n=27) of the combined total of insect prey. The percentage of diurnal insects among prey items varied across sites, ranging between 0.85% at Anduramba and 4.25% at Conondale Ra. In addition, eight diurnal insects were recorded among prey remains at Mt Molloy (3), Paluma (1) and Iron Ra. (4) (Table 1).

Diurnal insects taken were predominantly Lepidoptera (16) and Odonata (13), although a smaller number of Hemiptera, all cicadas (6), were captured (Table 1). All individuals taken were winged adults. In total, seven families of diurnal insects were taken by *R. megaphyllus* during the study. The Hesperiidae (skippers) was the most frequently taken family. Other insect orders were recorded among prey remains, but they did not include species that were definitely known to be diurnal.

POTENTIAL PREDATORS. A number of species of diurnal birds known to feed on bats (Young, 1980; Marchant & Higgins, 1993; Speakman et al., 1994) were sighted during incidental observations at the study sites. These species were: Collared Sparrowhawk *Accipiter cirrhocephalus* (Vieillot), Peregrine Falcon *Falco peregrinus* Tunstall, Australian Hobby *F. longipennis* Swainson, Nankeen Kestrel *F. cenchroides* Vigors & Horsfield, Laughing Kookaburra *Dacelo novaeguineae* (Hermann), Pied Butcherbird *Cracticus nigrogularis* (Gould), Grey Butcherbird *C. torquatus* (Latham) and Pied Currawong *Strepera graculina* (Shaw). Two of these species, Grey Butcherbird and Pied Currawong, were sometimes attracted to the entrances of roosts when bats were released during daylight.

EMERGENCE TIME OF BATS. The mean emergence time of the colony at Anduramba, which was located in woodland, was 29 minutes after sunset (1.62 SE). This emergence time was, on average, 9 minutes (3.34 SE) prior to darkness. Colony size during the counts ranged from 21 to 91 individuals. The mean emergence time of the colony at Conondale Ra., which was located in rainforest, was 4 minutes prior to sunset (2.08 SE). This emergence time was, on average, 39 minutes (3.79 SE) prior to darkness. Colony size during the counts ranged from 100 to 380 bats.

DISCUSSION

This study investigated the hypothesis that bats exhibit crepuscular activity as a means of gaining access to diurnal insects. *Rhinolophus megaphyllus*, a species that is active at dusk, did feed on diurnal insects. Current knowledge of the foraging ecology and auditory capacities of this species, and other members of its genus, indicates that diurnal insects were captured while they were active rather than while resting on vegetation at night. Also, none of the species of diurnal insects captured (Table 1) was observed roosting in disused mines. Therefore, bats probably did not capture diurnal insects in roosts.

The frequency of predation on diurnal insects pooled across the four roosts was one in every 30 prey items (3.25%). This frequency is low, although not unexpected given the short duration of dusk within the study area. In SE Queensland the time between sunset and the following sunrise ranges from a maximum of about 800 minutes in June to a minimum of 600 minutes in December. The duration of dusk, the time between sunset and dark, is only 30 to 45 minutes. Therefore, dusk represents between 4 and 8% of potential foraging time. The rate of predation on diurnal insects was thus lower than the proportion of available foraging time taken up by the dusk period.

Overall, the study provides preliminary support for the hypothesis that bats forage at dusk in order to gain access to diurnal insects. However, other explanations are possible. Bats may depart their roosts at dusk in order to commute to distant foraging areas which are only reached after dark. Alternatively, bats may forage on early flying nocturnal species during dusk, with diurnal species being captured incidentally. Clearly, more research is needed before definitive conclusions can be drawn.

The amount of predation on diurnal insects by *R. megaphyllus* varied between colonies. The lowest predation rate was in woodland at Anduramba (0.85%). The highest rate was in rainforest at Conondale Ra. (4.25%). The departure times of bats also differed between the two roosts. Bats at Anduramba began emerging 29 minutes after sunset, whereas those at Conondale Ra. began emerging 4 minutes prior to sunset. The difference in departure times was probably caused by the dense canopy of rainforest at Conondale Ra., which restricted the penetration of light at the mine entrance in the late afternoon. Thus bats emerged when light levels were low in rainforest adjacent to the roost, but still quite high in nearby open forest in which they foraged (C. Pavey, unpub. obs.). Earlier emergence at roosts with greater cover has been observed for other species of bats (e.g., Jones et al., 1995).

ACKNOWLEDGEMENTS

The authors thank the Department of Environment, Queensland, for providing both logistic support and permits to conduct the research. We thank the many people who provided able field assistance during the study. This paper has benefited considerably from constructive comments provided by Jens Rydell, Gareth Jones, Peter F.

Woodall, and Bradley S. Law. Financial support was provided by the Wet Tropics Management Authority, Ecological Society of Australia, Linnean Society of NSW, Royal Zoological Society of NSW, M.A. Ingram Trust, Australian Geographic Society and The University of Queensland. Both authors were in receipt of an Australian Postgraduate Research Award during the course of the study.

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